

Checklist

Annotated checklist of arthropod-pathogenic species in the Entomophthoromycotina (Fungi, Zoopagomycota) in North America

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Abstract

The subphylum Entomophthoromycotina (Phylum Zoopagomycota) includes many arthropod pathogens, some of which are renowned for their abilities to alter host behavior prior to death and cause epizootics that impact host populations. The last checklist of arthropod-pathogenic species in this group was published in 1963 and consisted of 39 species in a single genus. Since then, more species have been named, and their taxonomy has changed extensively. We have constructed an updated checklist for species of Entomophthoromycotina in North America; this checklist includes species in the continental United States, Canada, and Mexico. Data were compiled based on available published literature and metadata available from the ARSEF culture collection, adjusting names based on current taxonomy. In North America, the arthropod-pathogenic Entomophthoromycotina now include 80 species belonging to 14 genera, within two classes, plus one species in a form genus. This checklist provides a current framework for future studies of the biodiversity of this group of fungi.

Key words: Biodiversity, entomopathogenic fungi, Entomophthorales, mycodiversity, pathogen species list



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Introduction

Most species in the fungal subphylum Entomophthoromycotina (Phylum Zoopagomycota; Spatafora et al. 2016) are pathogens of arthropods. Many species in this group naturally cause epizootics (Pell et al. 2001), highlighting their potential use for biological control of arthropod pests. Species in this group are also renowned for altering the behavior of infected arthropod hosts in fixed, predictable patterns (de Bekker et al. 2021), including 'summit behavior' just prior to host death (e.g., Elya et al. 2018) or producing psychoactive metabolites to stimulate continued flight by spore-ejecting infected cicada hosts (Boyce et al. 2019).

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Despite their promising roles in the control of insect pests and their fascinating biology, relatively few studies have documented the biodiversity, distribution, and ecology of entomophthoralean fungi in natural ecosystems. Most inventories of species of arthropod-pathogenic fungi in the Entomophthoromycotina originate from Europe. Twenty-six species have been listed for Spain (Niell and Santamaria 2001), 24 for Sweden (Gustafsson 1965), 12 for Norway (Klingen et al. 2002), 29 for Austria (Barta et al. 2005; Tkaczuk et al. 2011), and 35 for the United Kingdom (www.mapmate.co.uk/checklist). The much higher counts for Switzerland (95; Keller 2008; S. Keller pers. comm.) and Poland (94; Sosnowska et al. 2004; Mułenko et al. 2008; Dubiel 2016) are consistent with the suggestion that this group of fungi is most diverse in central Europe (Keller 2008). However, this statement might be biased by the prolific work of researchers specifically studying the subject in that geographical area. Outside of Europe, lists of species have also been reported for China (79; Zha et al. 2016), Israel (31; Ben-Ze'ev 1993), the Philippines (19; Villacarlos and Mejia 2004; Villacarlos 2008), Argentina (16; López Lastra et al. 2019), and Australia (10; Glare and Milner 1987), as well as in several different publications from Mexico (Remaudière and Latgé 1985; Sanchez-Peña 1990, 2000).

For North America, Roland Thaxter published a comprehensive monograph on the family Entomophthoraceae in the United States in 1888, in which he reported on 26 species (Thaxter 1888). Following this, Charles (1941) reported 36 species in this group for North America, and in 1963, Hutchison reported 39 species of entomophthoralean fungi that occurred in North, Central, and South America and provided information about hosts and geographic distributions of these species. In the 21st century, a protochecklist of all nonlichenized fungi in North America included 38 species of arthropod-pathogens in the Entomophthoromycotina (Bates and Miller 2018). The protochecklist entries were based on herbarium specimens from the US (plus its territories), Canada, and Mexico, and in many instances, the names of arthropod pathogens that were included are not the currently accepted names.

Although there has not been an up-to-date summary of arthropod pathogens in North American species after 1963, the discovery, taxonomic changes, and research since that time have been prolific. It is very clear that an updated checklist is sorely needed; for example, the most recent protochecklist for all North American fungi does not use current taxonomic genera and species designations for this group (Bates and Miller 2018), certainly because this information might not be easy to find. Therefore, our goal with this annotated checklist was to present arthropod hosts and distributions for arthropod-pathogenic species in the Entomophthoromycotina that occur in North America, using the currently accepted taxonomy. This will facilitate continued progress in this field and summarize disparate observations as a compendium.

Materials and methods

Study area

This checklist of arthropod-pathogenic North American species includes records from the continental United States, Canada, and Mexico.

The data

Published records that were used to begin generating this checklist were found in Thaxter (1888), Charles (1941), Hutchison (1963), and Bałazy (1993). The catalogue of the USDA Agricultural Research Service Collection of Entomopathogenic Fungi (ARSEF 2020) was also used to search for North American records falling within the arthropod-pathogenic Entomophthoromycotina. Subsequently, search engines were used to explore records for additional North American species, using a recent worldwide list of species within the arthropod pathogens of the Entomophthoromycotina (Sacco and Hajek 2023). Personal communication records for R.A. Humber are from his notes regarding specimens in the Thaxter collection at the Farlow Herbarium, Harvard University. Throughout the checklist, only naturally occurring fungi associated with field-collected arthropod hosts were included. Samples from laboratory manipulations, often from studies of host specificity, have not been included.

Within the Entomophthoromycotina, extensive taxonomic reorganization has occurred in relatively recent years, and many generic names have changed. For example, in 1963, *Entomophthora* is given as the generic name for all 39 species in the Western Hemisphere (Hutchison 1963). However, for all except 4 of these species, the generic names have since changed. We used Humber (1989), Index Fungorum (http://www.indexfungorum.org), and MycoBank (Robert et al. 2005) to assist with all taxonomic decisions about fungi. We only include information from records with fungal identifications to the species level. For all arthropod hosts, only the currently accepted genus and species names are used.

For all records, hosts and distributions are provided with associated citations. For distributional information for North America, we generally referred to states or provinces but also provided citations for references where more specific details about collection site locations were found. For some records, only the name of the country was available. In at least one publication, the locations of species by country were not provided, and this record therefore could not be included (e.g., Remaudière et al. 1978). Two-letter, capitalized abbreviations of US states and Canadian provinces were used. For records from Mexico, we used 'conventional' abbreviations that are 2–4 letters long for states (https://en.wikipedia.org/wiki/Template:Mexico_State-Abbreviation_Codes). In all cases, the country name occurs alongside states or provinces. GPS coordinates for sites are not included, as for most entries, references are older, and GPS information was not available. Alternatively, descriptions of sites were too vague or broad for us to infer a GPS location. GPS information provided in more recent reports is available via the citations provided.

For information about hosts, only pathogens in the Entomophthoromycotina infecting arthropods were included (Sacco and Hajek 2023). For example, reports of vertebrate infections by *Conidiobolus coronatus* and reports of species only isolated from soil (e.g., many *Conidiobolus* spp.) were not included.

Many arthropod-pathogenic species in the Entomophthoromycotina have not been isolated into pure culture. Among those that have, numerous have been frozen and deposited in culture collections. The USDA-ARS entomopathogenic fungi collection (ARSEF) is the world's largest repository of these isolates, and we have indicated for each species whether a culture is available in ARSEF. We have not included GenBank accession numbers for numerous reasons, including that DNA data for most of these fungi are lacking or difficult to link to specimens, as many of these are older records prior to the DNA era. We can only confidently link accessions correctly to a few known specimens, and these are scarce. For those fungal species that have been sequenced, accession numbers can be found in the references cited or in GenBank.

References are always provided, but we did not exhaustively include references; if several references report a host/fungus association from the same state/province, we only included one of such references. Summaries were cited if these existed.

Results

Records for host species and distributions are reported below. For species with more extensive lists of hosts and distributions, detailed accounts are included in tabular form. For example, for some species reported from many states across much of North America, hosts and distribution are summarized below, but individual host species and specific collection locations are listed in tables. Species names below followed by an asterisk have arthropod pathogenic North American isolates in the ARSEF culture collection.

Class Neozygitomycetes
Order Neozygitales
Family Neozygitaceae
Neozygites

[1] Neozygites floridanus (J. Weiser & Muma) Remaud. & S. Keller, 1980

In the US, *N. floridanus* has been reported infecting six species of mites in the family Tetranychidae (Arachnida, Trombidiformes) in the southeastern US states, as well as IA, KS, PA, and TX (US) (Lopes Ribeiro et al. 2009) (Table 1). This species is frequently referred to as *N. floridana*, which is taxonomically incorrect.

Table 1. Recorded arthropod hosts of *Neozygites floridanus* in the US, all in the family Tetranychidae (Arachnida, Trombidiformes).

Host Species	Country	States	References
Eotetranychus sexmaculatus	US	FL	Lopes Ribeiro et al. 2009
Eutetranychus banksi	US	FL, TX	Pickett and Gilstrap 1986; Lopes Ribiero et al. 2009
Oligonychus pratensis	US	KS	Dick and Buschman 1995
Panonychus citri	US	FL	Lopes Ribiero et al. 2009
Tetranychus urticae	US	AL, GA, IA, KS, MS, NC, NY, SC	Lopes Ribiero et al. 2009; ARSEF 2020
Bryobia sp.	US	PA	C. Tkaczuk, unpubl. data
-	US	PA	C. Tkaczuk, unpubl. data

[2] Neozygites fresenii (Nowak.) Remaud. & S. Keller, 1980

On multiple aphid species (Hemiptera, Aphididae) from a broad distribution across the US, as well as ON (Canada) and Mexico (Fig. 1, Table 2).

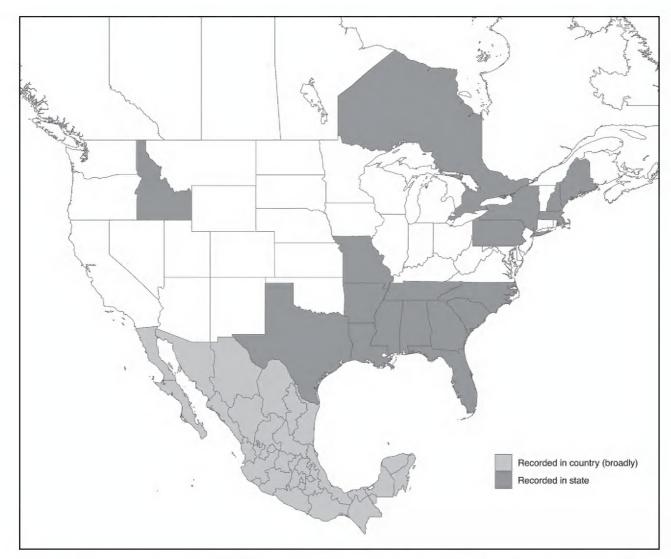


Figure 1. Distribution of recorded occurrences of *Neozygites fresenii* in the US, Canada, and Mexico (see references in Table 2). Dark gray = locations by state in the US or province in Canada; light gray = a record from an unspecified area within Mexico.

Table 2. Recorded arthropod hosts of Neozygites fresenii in the US, Canada, and Mexico, all hosts Hemiptera.

Host Family	Host Species	Country	States/Provinces	References
Aphididae	Aphis glycines	US	AR,NY	Nielsen and Hajek 2005; Galligan 2007
	Aphis gossypii	US	AL, AR, GA, LA, MS, MO, NC, SC, TN, TX	Sanchez-Peña 1993; Steinkraus et al. 1996
	Aphis gossypii	Mex	-	Remaudière and Latgé 1985
	Aphis pomi	US	MA, ME, NC	Thaxter 1888
	Aphis solitaria	Mex	-	Remaudière and Latgé 1985
	Aphis spiraecola	US	FL	Charles 1941
	Capitophorus elaeagni	Mex	-	Remaudière and Latgé 1985
	Myzus persicae	US	FL	Charles 1941
	Periphyllus lyropictus	US	NH	Charles 1941
	Schizaphis graminum	US	ID	Feng et al. 1990
	Schizolachnus piniradiatae	Can	ON	Soper and MacLeod 1963
	-	US	PA	C. Tkaczuk, unpubl. data
Pseudococcidae	Planococcus citri	US	LA	Charles 1941

[3] Neozygites fumosus (Speare) Remaud. & S. Keller, 1980

On the mealybug *Planococcus citri* (Hemiptera, Pseudococcidae) in FL and LA (US) (Speare 1922). This species is frequently referred to as *N. fumosa*, which is taxonomically incorrect.

[4] Neozygites lageniformis (Thaxt.) Remaud. & S. Keller, 1980

Infecting 'Aphides on *Betula populifolia*' and 'Solidago' in MA, ME, and NC (US) (Thaxter 1888), and infecting *Macrosiphum euphorbiae* and *Aphis nasturtii* (Hemiptera, Aphididae) in ME (US) (Shands et al. 1972).

[5] Neozygites parvisporus (D.M. MacLeod & K.P. Carl) Remaud. & S. Keller, 1980

On *Frankliniella* sp. (Thysanoptera, Thripidae) in BC (Mexico) (Remaudière and Latgé 1985). This species is frequently referred to as *N. parvispora*, which is taxonomically incorrect.

[6] Neozygites turbinatus (R.G. Kenneth) Remaud. & S. Keller, 1980

On *Cinara curvipes* (Hemiptera, Aphididae, Lachninae) in Jal (Mexico) (Remaudière and Latgé 1985). This species is frequently referred to as *N. turbinata*, which is taxonomically incorrect.

Class Entomophthoromycetes
Order Entomophthorales
Family Conidiobolaceae
Conidiobolus

[7] Conidiobolus coronatus (Constantin) A. Batko 1964*

On diverse insects, including termites (Isoptera, Kalotermitidae and Termitidae), aphids, and leafhoppers (Hemiptera), Diptera, Hymenoptera, and Thysanoptera. A truly polyphagous fungus, this species is also known to infect Collembola (Entognatha), Araneida, and Opiliones (Palpatores). It has been reported from across the US, Ver (Mexico), and AB (Canada) (Hutchison 1963; Matanmi et al. 1974; ARSEF 2020) (Table 3).

Table 3. Recorded arthropod hosts of Conidiobolus coronatus in the US, Canada, and Mexico.

Host Class	Host Order /Suborder	Host Family	Host Species	Country	States/ Provinces	References
Arachnida	Araneida	-	-	Can	AB	ARSEF 2020
	Opiliones/"Palpatores"	-	-	Can	AB	ARSEF 2020
Entognatha	Collembola	-	-	US	NC	ARSEF 2020
Insecta	Diptera	Anthomyiidae	Delia platura	US	WI	Matanmi et al. 1974
			Delia radicum	US	WI	Matanmi et al. 1974
		Bibionidae	Plecia nearctica	US	FL	Kish et al. 1974
		Sciaridae	Lycoriella ingenua	Mex	Ver	ARSEF 2020
	Hemiptera	Aphididae	Aulacorthum solani	US	ME	Harris 1948
			Macrosiphum euphorbiae	US	ME	Harris 1948
			Metopolophium dirhodum	US	ID	ARSEF 2020
			Myzus persicae	US	ME	Harris 1948
		Cercopidae	Aeneolamia albofasciata	Mex	Oax	Remaudiére and Latgé 1985
			Aeneolamia contigua	Mex	Tamps	Guzmán and Alcocer-Gómez 1972
		Cicadellidae	Empoasca fabae	US	NY	ARSEF 2020
	Hymenoptera	Formicidae	-	Can	AB	ARSEF 2020
	Isoptera	Kalotermitidae	-	US	CA, LA	Hutchison 1963
		Termitidae	-	US	CA, LA	Hutchison 1963
	Orthoptera	Acrididae	-	Mex	-	Remaudiére and Latgé 1985
	Thysanoptera	Thripidae	-	US	VT	ARSEF 2020
			Frankliniella occidentalis	US	FL	ARSEF 2020

Family Neoconidiobolaceae Neoconidiobolus

[8] Neoconidiobolus thromboides (Drechsler) B. Huang & Y. Nie, 2020*

Well known as an aphid (Hemiptera, Aphididae) pathogen: on numerous aphid hosts across the US and in AB, ON, and QC (Canada). It has also been reported from another hemipteran, the leafhopper *Empoasca fabae* in NY (US) (Hemiptera, Cicadellidae), a heleomyzid fly in ME (US) (Diptera, Heliomyzidae), and an acridid in MT (US) (Orthoptera, Acrididae) (ARSEF 2020; Castrillo and Harris-Shultz 2024). *Delia radicum* and *Delia platura* (Diptera, Anthomyiidae) were also reported infected in WI (US) (Matanmi et al. 1974) (Table 4).

Table 4. Recorded arthropod hosts of *Neoconidiobolus thromboides* in the US and Canada.

Host Order	Host Family	Host Species	Country	States/ Provinces	References
Diptera	Anthomyiidae	Delia platura	US	WI	Matanmi et al. 1974
		Delia radicum	US	WI	Matanmi et al. 1974
	Heliomyzidae	-	US	ME	ARSEF 2020
Hemiptera Aphididae	Aphis glycines	US	MN, NY	Nielsen and Hajek 2005	
		Diuraphis tritici	US	MT	Feng et al. 1991
		Macrosiphum euphorbiae	US	ME	ARSEF 2020
		Melanaphis sacchari	US	GA	Castrillo and Shultz 2024
		Metopolophium dirhodum	US	ID	ARSEF 2020
		Myzus persicae	US	FL, ME, WI	ARSEF 2020
		Schizaphis graminum	Can	AB	ARSEF 2020
		Sitobion avenae	US	ID	ARSEF 2020
		Therioaphis maculata	US	CA	ARSEF 2020
		Uroleucon sp.	Can	QC	ARSEF 2020
	Cicadellidae	Empoasca fabae	US	NY	ARSEF 2020
Orthoptera	Acrididae	-	US	MT	ARSEF 2020

Family Batkoaceae Batkoa

[9] Batkoa apiculata (Thaxt.) Humber, 1989*

Broad host range including four families of Lepidoptera (Erebidae, Noctuidae, Tortricidae, Geometridae), numerous aphid species (Hemiptera, Aphididae), leafhoppers (Hemiptera, Cicadellidae), a spittlebug (Hemiptera, Cercopidae), Scirtidae and Helotidae (Coleoptera), and nematocerans (Diptera). Collected across the northern US, as far south in the US as TN and NC but also in SLP (Mexico) (Thaxter 1888; Hutchison 1963; ARSEF 2020) (Table 5).

[10] Batkoa major (Thaxt.) Humber, 1989*

Initially, described from Ptilodactylidae (Coleoptera) in NC (US) by Thaxter (1888). Epizootics occurred in *Lycorma delicatula*, an invasive species in the Fulgoridae (Hemiptera) in PA (US) in 2018 (Clifton et al. 2019). Following field surveys of host range in PA and NY (US), confirmed infections were observed in 3 families of Coleoptera, 8 families of Diptera, 5 families of Hemiptera, 6 families of Lepidoptera, and 1 family of Psocomorpha (Gryganskyi et al. 2022a) (Table 6).

Table 5. Recorded arthropod hosts of Batkoa apiculata in the US and Mexico.

Host Order	Host Family/Suborder	Host Species/Subfamily	Country	States	References
Coleoptera	Cantharidae	-	Mex	Oax	Remaudière and Latgé 1985
	Scirtidae	-	US	TN	Hutchison 1963
Diptera Nematocera	Nematocera	-	US	ME, NC	Thaxter 1888
		-	Mex	Tamps	Remaudière and Latgé 1985
Hemiptera	Aphididae	Acyrthosiphon pisum	US	NY	ARSEF 2020
	Aphididae	Macrosiphum euphorbiae	US	ME	ARSEF 2020
	Aphididae	Myzus persicae	US	ME	ARSEF 2020
Aphididae Aphididae	Aphididae	Rhopalosiphum maidis	US	MT	ARSEF 2020
	Aphididae	Rhopalosiphum padi	US	CO	ARSEF 2020
	Cercopidae	Prosapia simulans	Mex	-	Remaudière and Latgé 1985
	Cicadellidae	-	US	NH, NY	ARSEF 2020
	Cicadellidae	Typhlocyba sp.	US	ME, NC	Thaxter 1888
Lepidoptera	Erebidae	Hyphantria cunea	US	ME, NC	Thaxter 1888
Er	Erebidae	listed as 'Deltoid sp.'	US	ME, NC	Thaxter 1888
	Geometridae	Petrophora sp.	US	ME, NC	Thaxter 1888
	Tortricidae	Tortrix sp.	US	ME, NC	Thaxter 1888

Table 6. Recorded arthropod hosts of Batkoa major in the US and Mexico.

Host Order	Host Family	Host Species	Country	States	References
Coleoptera	Cantharidae	Rhagonycha fraxini	US	NY	Gryganskyi et al. 2022a
		Rhagonycha sp.	US	NY	Gryganskyi et al. 2022a
	Elateridae	Athous brightwelli	US	NY	Gryganskyi et al. 2022a
	Ptilodactylidae	Ptilodactyla serricollis	US	NC	Thaxter 1888
	Tenebrionidae	Isomira sericea	US	NY	Gryganskyi et al. 2022a
Diptera	Anthomyiidae	-	US	NY	Gryganskyi et al. 2022a
	Dolichopodidae	Gymnopterus sp.	US	NY	Gryganskyi et al. 2022a
		Medetera sp.	US	PA	Gryganskyi et al. 2022a
		Thrypticus sp.	US	NY	Gryganskyi et al. 2022a
	Drosophilidae	Drosophila suzukii	US	TN	ARSEF 2020
	Heleomyzidae	Tephrochlamys rufiventris	US	NY	Gryganskyi et al. 2022a
	Lauxaniidae	Homoneura inserta	US	NY, PA	Gryganskyi et al. 2022a
	Milichiidae	Madiza glabra	US	PA	Gryganskyi et al. 2022a
	Psychodidae	-	US	NY	Gryganskyi et al. 2022a
	Rhagionidae	-	US	NY	Gryganskyi et al. 2022a
		Symphoromyia sp.	US	NY	Gryganskyi et al. 2022a
	Sciaridae	-	US	NY, PA	Gryganskyi et al. 2022a
Hemiptera	Achilidae	-	US	NY	Gryganskyi et al. 2022a
	Aphididae	Macrosiphum euphorbiae	US	ME	ARSEF 2020
	Cercopidae	Prosapia simulans	Mex	Chis, Tamps	Remaudiére and Latgé 1985
	Cicadellidae	-	US	NY	Gryganskyi et al. 2022a
		Empoasca fabae	US	NY	ARSEF 2020
	Cixiidae	Cixius sp.	US	NY	Gryganskyi et al. 2022a
	Derbidae	Apache degeeri	US	NY	Gryganskyi et al. 2022a
	Fulgoridae	Lycorma delicatula	US	PA	Gryganskyi et al. 2022a
Lepidoptera	Blastobasidae	-	US	NY	Gryganskyi et al. 2022a
	Crambidae	Eudonia sp.	US	NY	Gryganskyi et al. 2022a
	Erebidae	Lophocampa caryae	US	NY	Gryganskyi et al. 2022a
		Lymantria dispar	US	NY	Gryganskyi et al. 2022a
	Geometridae	Lambdina fiscellaria	US	NY	Gryganskyi et al. 2022a
	Oecophoridae	Fabiola edithella	US	NY	Gryganskyi et al. 2022a
	Tineidae	Dryadaula sp.	US	NY	Gryganskyi et al. 2022a
Psocoptera	Amphipsocidae	Polypsocus corruptus	US	NY	Gryganskyi et al. 2022a
	Psocomorpha	-	US	PA	Gryganskyi et al. 2022a

[11] Batkoa obscura (I.M. Hall & P.H. Dunn) Gryganskyi, 2022*

On numerous species of aphids in CA, NY, ID, MT, and ME (US) and QC (Canada) (Table 7).

Table 7. Recorded arthropod hosts of *Batkoa obscura* in the US, Canada, and Mexico, all in the family Aphididae (Hemiptera).

Host Species	Country	States/ Provinces	References
Acyrthosiphon pisum	US	NY	ARSEF 2020
Aphis nasturtii	US	ME	Shands et al. 1972
Aphis sp.	Can	QC	ARSEF 2020
Aulacorthum solani	US	ME	Shands et al. 1972
Capitophorus elaeagni	Mex	-	Remaudiére and Latgé 1985
Capitophorus shepherdiae	Mex	-	Remaudiére and Latgé 1985
Capitophorus xanthii	Mex	-	Remaudiére and Latgé 1985
Hyperomyzus lactucae	Mex	-	Remaudiére and Latgé 1985
Macrosiphum euphorbiae	US	ME	Shands et al. 1962
Macrosiphum spp.	Mex	-	Remaudiére and Latgé 1985
Metopolophium dirhodum	US	MT	Feng et al. 1991
Microparsus (Picturaphis) sp.	Mex	-	Remaudiére and Latgé 1985
Myzus persicae	US	ME	Shands et al. 1962
Myzus persicae	Mex	-	Remaudiére and Latgé 1985
Rhopalosiphum maidis	US	MT	Feng et al. 1991
Rhopalosiphum maidis	Mex	-	Remaudiére and Latgé 1985
Rhopalosiphum padi	Can	QC	ARSEF 2020
Rhopalosiphum padi	Mex	-	Remaudiére and Latgé 1985
Rhopalosiphum sp.	Mex	-	Remaudiére and Latgé 1985
Therioaphis maculata	US	CA	ARSEF 2020
Uroleucon ambrosiae	Mex	-	Remaudiére and Latgé 1985
Uroleucon sonchi	Mex	-	Remaudiére and Latgé 1985
Uroleucon sp.	Can	QC	ARSEF 2020
Uroleucon sp.	Mex	-	Remaudiére and Latgé 1985

[12] Batkoa papillata (Thaxt.) Humber, 1989

On 'several minute gnats' (Diptera, Nematocera) from NH and NC (US). In North America, known only from these initial collections by Thaxter (1888).

Family Entomophthoraceae Subfamily Entomophthoroideae *Arthrophaga*

[13] Arthrophaga myriapodina K.T. Hodge & A.E. Hajek, 2017

Reported from three species of millipedes (Myriapodina, Polydesmidae): *Apheloria virginiensis corrugata*, *Nannaria* sp., and *Boraria infesta* in MA, MD, NC, NY, PA, and VA, Washington DC (US), and southern ON (Canada) (Hodge et al. 2017).

Entomophaga

[14] Entomophaga aulicae (E. Reichardt) Humber, 1984 (aulicae species complex)*

Entomophaga aulicae is a complex of morphologically identical species infecting only Lepidoptera, within which only *E. maimaiga* has been named as a separate species (treated below). Aside from *E. maimaiga*, fungal populations belonging to the *E. aulicae* complex infect lepidopteran species in the Noctuidae, Erebidae, Geometridae, Tortricidae, Lasiocampidae, Notodontidae, Sphingidae, and Saturniidae families from around the US and Canada (FPMI 1990; Walsh 1996; Speare and Colley 1912; ARSEF 2020). An invasive species in the Hesperiidae (Lepidoptera) in QC (Canada) was also infected (McNeil and MacLeod 1982). Within the complex, genetic diversity has been detected, with two groups occurring in North America. Pathotype I includes hosts in the Geometridae, Tortricidae, Notodontidae, and Saturniidae from BC, ON, and NF (Canada) and ME, NY, and VT (US). Pathotype II includes species in the Noctuidae and Erebidae in GA, CA (US), and ON (Canada) (Hajek et al. 1996b; Walsh et al. 1990; Walsh 1996) (Table 8).

Table 8. Recorded arthropod hosts of *Entomophaga aulicae* in the US, Canada, and Mexico, with all hosts in the order Lepidoptera.

Host Family	Host species	Country	States/ Provinces	References	Group
Erebidae	Catocala sp.	US	СТ	Speare and Colley 1912	-
	Estigmene acrea	US	СТ	Speare and Colley 1912	-
	Estigmene acrea	Mex	Son	Young and Sifuentes 1959	-
	Euchaetes egle	US	-	Speare and Colley 1912	-
	Euproctis chrysorrhoea	US	MA, ME	Kirkland 1906; Boyd et al. 2021	-
	Hypena scabra	US	SC	Kalkar and Carner 2005	-
	Hyphantria cunea	Can	ON	Walsh et al. 1990	ll II
	Orgyia antiqua nova	Can	NF	Thaxter 1888	-
	Orgyia leucostigma	Can	NS	van Frankenhuyzen et al. 2002	-
	Orgyia vetusta	US	CA	Hajek et al. 1996b	ll II
	Pyrrharctia isabella	US	ME	Hitchings 1908	-
	Spilosoma virginica	US	OH, TX	Webster 1894; Mitchell 1919	-
Geometridae	Epirrita autumnata	Can	BC	FPMI 1990	-
	Lambdina fiscellaria	Can	BC, NF	Walsh et al. 1990; Hajek et al. 1996b	I
	Nepytia freemani	Can	BC	FPMI 1990	-
	Rheumaptera hastata	Can	ON	Walsh et al. 1990	I
	Sabulodes griseata	Can	BC	ARSEF 2020	-
Lasiocampidae	Malacosoma americanum	US	СТ	Speare and Colley 1912	-
	Malacosoma disstria	US	NY	ARSEF 2020	-
Noctuidae	Agrotis sp.	US	СТ	Thaxter 1891	-
	Amphipyra pyramidoides	US	-	Speare and Colley 1912	-
	Helicoverpa zea	US	GA	Hamm 1980	-
	?Heliothis sp.	US	GA	Walsh et al. 1990	П
	Heliothis virescens	US	GA	Hamm 1980	-
	Lithophane sp.	US	СТ	Thaxter 1891	-
	Mamestra sp.	US	СТ	Thaxter 1891	-
	Mythimna sp.	Can	ON	ARSEF 2020	-
	Spodoptera frugiperda	US	GA	Hamm 1980	-
Nolidae	Nola cereella	US	GA	Hamm 1980	-

Host Family	Host species	Country	States/ Provinces	References	Group
Notodontidae	Cecrita biundata	Can	ON	ARSEF 2020	
	Cecrita guttivitta	US	NY, VT	Hajek et al. 1991; 1996b	I
	Ellida caniplaga	Can	ON	ARSEF 2020	-
Saturniidae	Dryocampa rubicunda	Can	ON	Walsh et al. 1990	I
Sphingidae	-	US	ME	FPMI 1990	-
	Manduca quinquemaculata	US	CT	Thaxter 1891	-
	Manduca sexta	US	CT	Thaxter 1891	-
	Pachysphinx modesta	US	ME	Farlow Herbarium unpubl. data	-
	Eumorpha fasciata	US	FL	ARSEF 2020	-
Tortricidae	Choristoneura fumiferana	US	ME	Walsh et al. 1990	
	Choristoneura fumiferana	Can	NF, ON	Walsh et al. 1990	I
	Choristoneura occidentalis	Can	BC	Hajek et al. 1996b	I

[15] Entomophaga batkoi (Bałazy) S. Keller, 1888

On a species in the Phalangidae in ME (US) (R.A. Humber pers. comm.).

[16] Entomophaga calopteni (Bessey) Humber, 1989 (E. grylli species complex)*

A member of the *Entomophaga grylli* species complex, also known as Pathotype 2. Infects species in the Acrididae, with most infections in the subfamily Melanoplinae, although lower levels of infection have been found in the subfamilies Oedopodinae and Gomphocerinae. Reported from AZ, IA, KS, MT, ND, SD, and WY (US), AB and SK (Canada), and NL and Coah (Mexico) (Thaxter 1888; Soper et al. 1983; Erlandson et al. 1988; Bidochka et al. 1995, 1996; Casique-Valdes et al. 2012, 2022; ARSEF 2020).

[17] Entomophaga grylli Pathotype I (Fresen.) A. Batko, 1964 (E. grylli species complex)*

A member of the *Entomophaga grylli* species complex, also known as Pathotype 1 or *E. macleodii* (an unpublished name). Principally infects grasshopper species in the subfamily Oedopodinae (Acrididae), although also known to infect Gomphocerinae and occasionally Melanoplinae. Reported from AZ, ND, NY, MT, and OR (US), and AB, ON, and SK (Canada), and Coah (Mexico) (Bidochka et al. 1996; Casique-Valdes et al. 2012, 2022; Kistner and Belovsky 2013; ARSEF 2020).

[18] Entomophaga kansana (J.A. Hutchison) A. Batko, 1964

Reported from Calliphoridae, Sarcophagidae, Muscidae, and Tachinidae (Diptera) near Lawrence, KS (US) (Hutchison 1962).

[19] Entomophaga maimaiga Humber, Shimazu & R.S. Soper, 1988 (aulicae species complex)*

Entomophaga maimaiga is a North Asian species only infecting Lepidoptera, accidentally introduced to North America, probably from Japan, at some time after 1971, but before 1989 (Weseloh 1998; Nielsen et al. 2005). Principal hosts are larvae of *Lymantria dispar* (Lepidoptera, Erebidae). Surveys of naturally occurring host specificity documented low levels of infections in 3 of 7 lymantriines (Hajek

et al. 2004). Rare infections also occurred in *Catocala ilia* (Erebidae) and *Malacosoma disstria* (Lasiocampidae) (Hajek et al. 1996a), *Agrochola bicolorago* (Noctuidae); an unidentified gelechiid (Lepidoptera) was also infected (Hajek et al. 2000). *E. maimaiga* was discovered in 1989 in seven northeastern US states (Hajek et al. 1990) and has since spread (naturally and with human assistance)



Figure 2. Distribution of recorded occurrences of *Entomophaga maimaiga* in the US and Canada, by state and province (Hajek et al. 2021; S. Picq pers. comm.).

into a total of 19 US states (Hajek et al. 2021). E. maimaiga has also been reported from ON and QC (Canada) (Nealis et al. 1999, S. Picq pers. comm.) (Fig. 2).

[20] Entomophaga tabanivora (J.F. Anderson & Magnar.) Humber, 1989

On *Tabanus nigrovittatus* and *Atylotus thoracicus* (Diptera, Tabanidae) in MA and NY (US) (Anderson and Magnarelli 1979; Mullens et al. 1983).

[21] Entomophaga tenthredinis (Fresen.) A. Batko, 1964

On sawfly larvae (Hymenoptera, Tenthredinidae), including *Pristiphora erichsonii* in ON (Canada), larvae of an unidentified tenthredinid species in ME (US), and the introduced pine sawfly, *Diprion similis*, in WI (US) (Thaxter 1888; Klein and Coppel 1973; FPMI 1990).

Entomophthora

[22] Entomophthora chromaphidis O.F. Burger & Swain, 1918

An aphid pathogen (Hemiptera, Aphididae) on *Chromaphis juglandicola* in CA (Burger and Swain 1918), the cereal aphids *Metopolophium dirhodum* in ID, WA (US) and *Sitobion avenae* in ID (US) (Humber and Feng 1991), *Myzus per-*

sicae in ID (Kish et al. 1994), and Aphis glycines in NY (US) (Nielsen and Hajek 2005). Also reported on Psocus sp. (Psocodea, Psocidae) in CA (US) (Burger and Swain 1918). At least some of the entries under E. planchoniana (Table 9) could instead be E. chromaphidis (see Humber and Feng 1991; Barta and Cagáň 2006); further study is necessary.

[23] Entomophthora culicis (A. Braun) Fresen., 1858

Reported by Thaxter (1888) on Diptera: "Culex [Culicidae], and numerous genera of minute flies or gnats" in MA, ME, and NH. On unidentified midges (Chironomidae) in NY (US) (Kramer 1981b) and unidentified black flies (Simuliidae) in AB (Canada) (Shemanchuk and Humber 1978).

[24] Entomophthora erupta (Dustan) I.M. Hall, 1959

On Miridae (Hemiptera): *Neolygus communis, Adelphocoris lineolatus, Irbisia solani, Lygocoris pabulinus*, and *Plagiognathus* sp. in NS (Canada) (Dustan 1924), and *I. solani* in CA (US) (Hall 1959). Also reported from *A. lineolatus* from NY (US) (Wheeler 1972).

[25] Entomophthora muscae (Cohn) Fresen., 1856*

Entomophthora muscae is a species complex of morphologically similar species infecting Diptera, including from 4 to 8 described species (Elya and De Fine Licht 2021). Three species within the complex occur in North America: *E. muscae sensu stricto* (s.s), *E. scatophagae* (treated separately), and *E. schizophorae* (treated separately). *Entomophthora muscae* s.s infects *Musca domestica* (Muscidae) in CA, NY, NC, and NE, and probably across most of the US and Canada, and in Coah (Mexico) (Sanchez-Peña unpubl. observations). Also on *Coenosia tigrina* (Muscidae) and *Delia radicum* (Anthomyiidae) in NC (US) (Gryganskyi et al. 2013), and six species of *Drosophila* (Drosophilidae) in CA (US): *Drosophila melanogaster*, *D. simulans*, *D. hydei*, *D. immigrans*, *D. pseudoobscura*, *D. repleta* (Elya et al. 2018). Further studies of hosts and distributions of the different members of this species complex in North America are necessary.

[26] Entomophthora planchoniana Cornu, 1873

On diverse species of aphids (Aphididae) across the US and Mexico (Table 9). However, at least some of the entries under *E. planchoniana* in Table 9 could instead be *E. chromaphidis* (see Humber and Feng 1991; Barta and Cagáň 2006); further study is necessary.

Table 9. Recorded arthropod hosts of *Entomophthora planchoniana* in the US and Mexico, with all hosts in the family Aphididae (Hemiptera).

Host Species	Country	States	References	
Acyrthosiphon malvae	Mex	-	Remaudière and Latgé 1985	
Acyrthosiphon pisum	Mex	Mex - Remaudière and Latgé		
Aphis asclepiadis	Mex	ex - Remaudière and Latgé 19		
Aphis coreopsidis	Mex	- Remaudière and Latgé 19		

Host Species	Country	States	References
Aphis fabae	Mex	-	Remaudière and Latgé 1985
Aphis gossypii	Mex	-	Remaudière and Latgé 1985
Aphis lugentis	Mex	-	Remaudière and Latgé 1985
Aphis nasturtii	US	ME	Shands et al. 1972
Aphis solitaria	Mex	-	Remaudière and Latgé 1985
Aphis spiraecola	Mex	-	Remaudière and Latgé 1985
Aulacorthum solani	US	ME	Shands et al. 1972
Brevicoryne brassicae	Mex	-	Remaudière and Latgé 1985
Capitophorus elaeagni	Mex	-	Remaudière and Latgé 1985
Capitophorus shepherdiae	Mex	-	Remaudière and Latgé 1985
Capitophorus xanthii	Mex	-	Remaudière and Latgé 1985
Chaetosiphon fragaefolii	US	CA	Dara 2017
Cryptomyzus galeopsidis	US	ME	Shands et al. 1962
Hayhurstia atriplicis	Mex	-	Remaudière and Latgé 1985
Hyperomyzus sp.	Mex	-	Remaudière and Latgé 1985
Latgerina orizabaensis	Mex	-	Remaudière and Latgé 1985
Macrosiphum euphorbiae	US	ME	Shands et al. 1962
Macrosiphum spp.	Mex	-	Remaudière and Latgé 1985
Melanocallis caryaefoliae	US	GA	Ekbom and Pickering 1990
Metopolophium dirhodium	US	ID	Feng et al. 1991
Metopolophium dirhodium	Mex	BC	Remaudière and Latgé 1985
Monellia caryella	US	GA	Ekbom and Pickering 1990
Monelliopsis pecanis	US	GA	Ekbom and Pickering 1990
Myzus ornatus	Mex	-	Remaudière and Latgé 1985
Myzus persicae	US	ME	Shands et al. 1962
Myzus persicae	Mex	-	Remaudière and Latgé 1985
Obtusicauda sp.	Mex	BC	Remaudière and Latgé 1985
Rhopalosiphum maidis	US	ID	Feng et al. 1991
Rhopalosiphum maidis	Mex	Coah	Sanchez-Peña 2000
Rhopalosiphum padi	Mex	BC	Remaudière and Latgé 1985
Rhopalosiphum padi	Mex	-	Remaudière and Latgé 1985
Rhopalosiphum sp.	Mex	-	Remaudière and Latgé 1985
Sitobion avenae	US	ME	Shands et al. 1962
Uroleucon ambrosiae	Mex	-	Remaudière and Latgé 1985
Uroleucon sonchi	Mex	-	Remaudière and Latgé 1985
Uroleucon sp.	Mex	-	Remaudière and Latgé 1985
Utamphorophora crataegi	Mex	-	Remaudière and Latgé 1985

[27] Entomophthora scatophagae Giard, 1888

A member of the *E. muscae* species complex (Jensen et al. 2006). On *Scato-phaga stercoraria* (Diptera, Anthomyiidae) in NY (Steinkraus and Kramer 1988).

[28] Entomophthora schizophorae S. Keller & Wilding, 1988

A member of the *E. muscae* species complex, infecting only Diptera (Elya and De Fine Licht 2021). Isolates from NE and NY (US) infect *Pollenia rudis* (Diptera, Polleniidae), and both also infect *Musca domestica*, although at lower prevalence (Steinkraus et al. 1993a; Watson et al. 1993; Six and Mullens 1996). Also, infects *Hylemya* sp. (Anthomyiidae) in PA (US) (C. Tkaczuk unpubl. data).

Eryniopsis

[29] Eryniopsis caroliniana (Thaxter) Humber, 1984

On Tipula sp. (Diptera, Tipulidae) in NC (US) (Thaxter 1888).

[30] Eryniopsis lampyridarum (Thaxter) Humber, 1984

On Chauliognathus pensylvanicus and Chauliognathus marginatus (Coleoptera, Cantharidae) in AR, MD, KS, NC, PA, SC, and VA (US) (Thaxter 1888; Carner 1980; Steinkraus et al. 2017) (Fig. 3). Also, on Chauliognathus sp. in Coah (Mexico) (RI Torres-Acosta & S. Sanchez-Peña, unpubl. observation: https://www.youtube.com/watch?v=NRBO7zc1J-o).

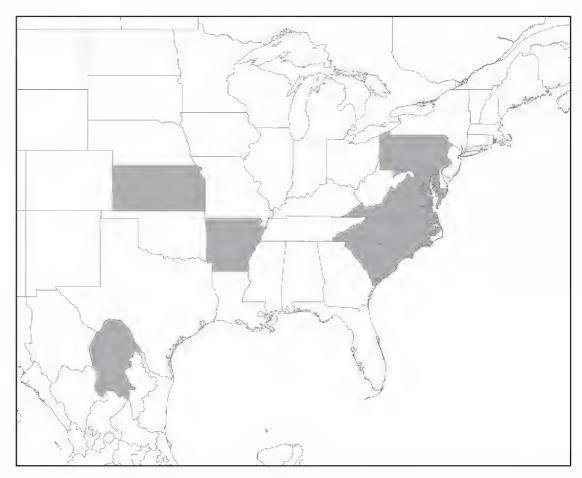


Figure 3. Distribution of recorded occurrences of *Eryniopsis lampyridarum* in the US and Mexico, by state (see references in the text).

Massospora

[31] Massospora cicadina Peck, 1878*

On species of the genus *Magicicada* (Hemiptera, Cicadidae) in the eastern US (Macias et al. 2020).

[32] Massospora diceroproctae R.S. Soper, 1974

On Diceroprocta delicata, Diceroprocta cinctifera, Diceroprocta vitripennis, and Diceroprocta biconica (Hemiptera, Cicadidae) in TX (and possibly LA, FL) (US) (Macias et al. 2020).

[33] Massospora fidicinae R.S. Soper, 1974

On Fidicina sp. (Hemiptera, Cicadidae) in Chis (Mexico) (Macias et al. 2020).

[34] Massospora levispora R.S. Soper, 1963

On Okanagana rimosa and Okanagana sperata (Hemiptera, Cicadidae) in CA (US) and ON (Canada) and Platypedia putnami (Hemiptera, Cicadidae) in CA, NM, and UT (US) (Macias et al. 2020).

[35] Massospora spinosa Cif., A.A. Machado & Vittal, 1956

On Quesada gigas (Hemiptera, Cicadidae) in NL (Mexico) (Macias et al. 2020).

Orthomyces

[36] Orthomyces aleyrodis Steinkr., Humber & Oliv., 1998

On *Trialeurodes abutiloneus* (Hemiptera, Aleyrodidae) in AL (US) (Steinkraus et al. 1998).

Subfamily Erynioideae *Erynia*

[37] *Erynia aquatica* (J.F. Anderson & Ringo ex J.F. Anderson & Anagnost.) Humber, 1981*

On larvae and pupae of Culicidae (Diptera) in the US: Aedes canadensis (CT, RI), Culiseta morsitans (CT), Aedes stimulans (NY), Aedes fitchii (NY), Aedes cantator (CT), Aedes sp. (NY) (Anderson and Ringo 1969; Molloy and Wraight 1982; Andreadis and Magnarelli 1983; Steinkraus and Kramer 1989; Christie 1996; ARSEF 2020).

[38] Erynia conica (Nowak.) Remaud. & Hennebert, 1980*

On Chironomidae, Chaoboridae, Simuliidae, and Tipulidae (Diptera) in NC, NH, and NY (US) (Thaxter 1888; Cuebas-Incle 1992; ARSEF 2020). On Simuliidae (Diptera) in QC (Canada): Simulium venustum complex, Simulium verecundum/rostratum, Simulium vittatum complex (Nadeau et al. 1994).

[39] Erynia curvispora (Nowak.) Remaud. & Hennebert, 1980*

Reported from adult *Simulium decorum* (Diptera, Simuliidae) in NY (US) and QC (Canada) (Kramer 1983; Nadeau et al. 1994), *Aedes triseriatus* (Diptera, Culicidae) in ME (US), and unidentified *Simulium* in NY (US) and QC (Canada) and Trichoptera in QC (Canada) (ARSEF 2020).

[40] Erynia gracilis (Thaxter) Remaud. & Hennebert, 1980

On "very minute gnats" (Diptera) in NC (US) (Thaxter 1888).

[41] Erynia ovispora (Nowak.) Remaud. & Hennebert, 1980

On a 'small gnat attached to bark' in TN (Diptera) (US) (R.A. Humber pers. comm.).

[42] Erynia rhizospora (Thaxter) Remaud. & Hennebert, 1980*

On Neuroptera and "several genera" of adult Phryganeidae (Trichoptera) in ME and NC (US) (Thaxter 1888). Also reported on Trichoptera in NY (US) (ARSEF 2020).

[43] Erynia sepulchralis (Thaxter) Remaud. & Hennebert, 1980*

On unidentified adult crane flies (Diptera, Tipulidae) in western NC and eastern TN (US) (Thaxter 1888), and on *Tipula caloptera* in NY (US) (Kramer 1980).

[44] Erynia variabilis (Thaxter) Remaud. & Hennebert, 1980

On 'minute gnats of various genera' in NC (Diptera) (US) (Thaxter 1888).

Pandora

[45] Pandora americana (Thaxter) S. Keller, 2007

On Diptera: Musca domestica (Muscidae), Calliphora vomitoria, and Lucilia caesar (Calliphoridae) and 'numerous other large flies.' Common in New England and less common in NC (US) (Thaxter 1888). Also reported in the US from Calliphora sp. (WI), C. vomitoria (AL), Phormia regina (TX) (Calliphoridae), and Muscina stabulans (TN) (Muscidae) (Charles 1941).

[46] Pandora blissi (G. Lakon) D.M. MacLeod & Müller-Kögler, 1973; nomen dubium

On the chinch bug, *Blissus leucopterus* (Hemiptera, Blissidae) in IA, IL, KS, MN, and OH (Billings and Glenn 1911). This species was initially placed in the genus *Empusa* by Thaxter (Gillette 1888). The 1888 species description was minimal (Gillette 1888), and no types were designated (but 'co-types' are present at Harvard). The provisional genus *Pandora* is based on ongoing evaluation of museum specimens.

[47] Pandora blunckii (G. Lakon ex G. Zimm.) Humber, 1989*

On *Plutella xylostella* (Lepidoptera, Plutellidae) in Gto. (Mexico) (ARSEF 2020) and on Diptera (possibly Sciaridae) in NY (US) (ARSEF 2020).

[48] Pandora bullata (Thaxt. & D.M. MacLeod ex Humber) Humber, 1989

On Calliphoridae (Diptera): including *Phormia regina*, *Lucilia sericata*, *Proto-phormia terraenovae*, *Calliphora vomitoria*, and perhaps other *Calliphora* spp. and Sarcophagidae (Diptera): *Sarcophaga aldrichi* in ON (Canada) and NY, MI, and MA (US) (MacLeod et al. 1973; Kramer 1979; Nielsen et al. 2001).

[49] Pandora delphacis (Hori) Humber, 1989*

On Hemiptera: Spissistilus festinus (Hemiptera, Membracidae) in AL, AR (US) (Miller and Harper 1987; ARSEF 2020), and Empoasca fabae (Hemiptera, Cicadellidae) and Miridae in NY (ARSEF 2020).

[50] Pandora dipterigena (Thaxter) Humber, 1989*

On Diptera: "small Tipulidae; other small flies or gnats belonging especially to the Mycetophilidae" in MA, ME, NC, and NH (US) (Thaxter 1888), unknown

dipterans in ME and NY (US) (ARSEF 2020), and nematocerans in Mich. (Mexico) (Remaudière and Latgé 1985).

[51] Pandora echinospora (Thaxter) Humber, 1989

On *Minettia duplicata* (Diptera, Lauxaniidae) and 'rarely other smaller Diptera' in ME, NH, and NC (US) (Thaxter 1888).

[52] Pandora formicae (Humber & Bałazy) Humber, 1989

On Formicinae (Hymenoptera, Formicidae) in ME (US) (R.A. Humber pers. comm.).

[53] Pandora gammae J. Weiser ex. Humber, 1989

On noctuid larvae (Lepidoptera): *Chrysodeixis includens* in AL and GA (US) in GA (US) and Tamps (Mexico) and *Trichoplusia ni* in AL (US) and Coah (Mexico) (Harper and Carner 1973; Newman and Carner 1975; Gilreath et al. 1986; Sanchez-Peña 1990, 2000). Also on *Mocis* sp. in NL and Coah (Mexico) (S.R. Sanchez-Peña unpubl. data).

[54] Pandora gastropachae (Racib.) Hajek & Gryganskyi, 2024*

In hardwood forests on *Malacosoma disstria* (Lepidoptera, Lasiocampidae), ranging from BC to QC (Canada) and ME to FL and AL (US) (Filotas et al. 2003).

[55] Pandora gloeospora (Vuillemin) Humber, 1989*

On Lycoriella mali (Diptera, Sciaridae) in mushroom production facilities in MD, DE, and southeastern PA (US) (Miller and Keil 1990, AP Gryganskyi pers. comm.) and cadavers producing conidia found on oyster mushrooms (*Pleurotus* sp.) in FL (US) (MW Miller pers. comm.).

[56] Pandora heteropterae (Bałazy) S. Keller, 2005*

On Lygus lineolaris (Hemiptera, Miridae) in AR (US) (Hannam and Steinkraus 2010).

[57] Pandora ithacensis (Kramer) Hajek & Gryganskyi, 2024*

On Diptera: Symphoromyia hirta and Rhagio mystaceus (Rhagionidae) and Empis obesa (Empididae) in NY (US) (Kramer 1981a) and an unidentified rhagionid in PA (US) (C. Tkaczuk unpubl. data).

[58] Pandora montana (Thaxter) Hajek & Gryganskyi, 2024

On Diptera on the alpine summit of Mt. Washington, NH (US), infecting "minute gnats, apparently *Chironomus* sp." (Thaxter 1888).

[59] Pandora muscivora (J. Schröt.) S. Keller, 2005

On Syrphus sp. (Diptera, Syrphidae) in ME (US) (MyCoPortal 2024).

[60] Pandora neoaphidis (Remaud. & Hennebert) Humber, 1989*

On diverse aphids (Hemiptera, Aphididae) across the US, Mexico, and QC (Canada). In addition, single records of *Lygus* sp. (Hemiptera, Miridae) in NY (US) (ARSEF 2020) and *Aeneolamia albofasciata* (Hemiptera, Cercopidae) in Mexico (Remaudière and Latgé 1985) (Table 10). These last records of this fungus on spittlebugs and mirids should be reconsidered due to the unambiguous nature of this fungus as a specialized aphid pathogen, and the brief and rather incomplete description in these records.

Table 10. Recorded arthropod hosts of Pandora neoaphidis in the US, Canada, and Mexico, all hosts in the order Hemiptera.

Host Family	Host Species	Country	States/ Provinces	References
Aphididae	Acyrthosiphon kondoi	US	CA	Pickering and Gutierrez 1991
	Acyrthosiphon pisum	US	CA, GA, ID, IL, MN, NY, PA, WA	Folsom 1909; Pickering et al. 1989; Pickering and Gutierrez 1991; ARSEF 2020; C. Tkaczuk unpubl. data
	Acyrthosiphon pisum	Mex	-	Remaudière and Latgé 1985
	Aphis asclepiadis	Mex	-	Remaudière and Latgé 1985
	Aphis coreopsidis	Mex	-	Remaudière and Latgé 1985
	Aphis fabae	US	WA	ARSEF 2020
/	Aphis fabae	Mex	-	Remaudière and Latgé 1985
	Aphis glycines	US	NY	ARSEF 2020; Nielsen and Hajek 2005
	Aphis gossypii	Mex	-	Remaudière and Latgé 1985
Ap	Aphis lugentis	Mex	-	Remaudière and Latgé 1985
	Aphis solitaria	Mex	-	Remaudière and Latgé 1985
	Aphis sp.	Can	QC	ARSEF 2020
	Aphis sp.	US	WA	ARSEF 2020
	Aphis spiraecola	Mex	-	Remaudière and Latgé 1985
	Aulacorthum solani	US	ME	Shands et al. 1972
	Brachycaudus helichrysi	Mex	-	Remaudière and Latgé 1985
	Brachyunguis tetrapteralis	Mex	-	Remaudière and Latgé 1985
	Brevicoryne brassicae	Mex	-	Remaudière and Latgé 1985
	Capitophorus elaeagni	Mex	-	Remaudière and Latgé 1985
	Capitophorus shepherdiae	Mex	-	Remaudière and Latgé 1985
	Capitophorus xanthii	Mex	-	Remaudière and Latgé 1985
	Cavariella hendersoni	Mex	-	Remaudière and Latgé 1985
	Diuraphis noxia	US	CO, ID	ARSEF 2020; Feng et al. 1990
	Hayhurstia atriplicis	Mex	-	Remaudière and Latgé 1985
	Hyperomyzus lactucae	Mex	-	Remaudière and Latgé 1985
	Hyperomyzus sp.	Mex	-	Remaudière and Latgé 1985
	Illinoia sp.	Mex	-	Remaudière and Latgé 1985
	Impatientinum americanum	Mex	-	Remaudière and Latgé 1985
	Macrosiphum euphorbiae	US	FL, ID, ME	ARSEF 2020; Feng et al. 1990
	Macrosiphum spp.	Mex	-	Remaudière and Latgé 1985
	Melanaphis sacchari	Mex	Coah	ARSEF 2020
	Metopolophium dirhodum	US	ID, MT	ARSEF 2020; Feng et al. 1990, 1991
	Myzus ornatus	Mex	-	Remaudière and Latgé 1985
	Myzus persicae	US	AR, ID, ME, VA, WA	Harris 1948; Elkassabany et al. 1992; Kish et al. 1994; Dara and Semtner 200
	Myzus persicae	Mex	/ 113, 10, 141E, 47, 44A	Remaudière and Latgé 1985

Host Family	Host Species	Country	States/ Provinces	References	
Aphididae	Myzus persicae nicotianae	US	KY, VA	ARSEF 2020; Dara and Semtner 2001	
	Rhapalosiphum padi	US	ID	Feng et al. 1990	
	Rhodobium porosum	Mex	-	Remaudière and Latgé 1985	
	Rhopalosiphum maidis	US	ID, MT	Feng et al. 1990, 1991	
	Rhopalosiphum maidis	Mex	-	Remaudière and Latgé 1985	
	Rhopalosiphum padi	Mex	-	Remaudière and Latgé 1985	
	Rhopalosiphum sp.	Mex	-	Remaudière and Latgé 1985	
	Schizaphis graminum	US	ID	ARSEF 2020; Feng et al. 1990	
	Schizaphis graminum	Mex	-	Remaudière and Latgé 1985	
	Sibobion avenae	US	ID	Feng et al. 1990	
	Sitobion sp.	Mex	-	Remaudière and Latgé 1985	
	Uroleucon ambrosiae	Mex	-	Remaudière and Latgé 1985	
	Uroleucon sonchi	Mex	-	Remaudière and Latgé 1985	
	Uroleucon sp.	Can	QC	FPMI 1990	
	Uroleucon sp.	Mex	-	Remaudière and Latgé 1985	
	Utamphorophora crataegi	Mex	-	Remaudière and Latgé 1985	
	Wahlgreniella arbuti	Mex	-	Remaudière and Latgé 1985	
Cercopidae	Aenolamia albofasciata	Mex	-	Remaudière and Latgé 1985	
Miridae	Lygus sp.	US	NY	ARSEF 2020	

[61] Pandora nouryi (Remaud. & Hennebert) Humber, 1989*

On aphids (Hemiptera: Aphididae) on potato in ME (US) (ARSEF 2020).

[62] Pandora pieris (Z.Z. Li & Humber) Hajek & Gryganskyi, 2024*

On larvae of *Pieris rapae* (Lepidoptera, Pieridae) in NY (US) (Li and Humber 1984).

[63] Pandora sylvestris Hajek & Gryganskyi, 2024

On larvae of *Lophocampa caryae* (Lepidoptera, Erebidae) from MI and VT (US) (Hajek et al. 2024a).

[64] Pandora virescens (Thaxter) Hajek & Gryganskyi, 2024

On Noctuidae (Lepidoptera): *Mythimna unipuncta* in AR (US), *Dargida procinctus* in OR (US), and *Ochropleura fennica* in ON (Canada) (Steinkraus et al. 1993b).

[65] Pandora vomitoriae (Rozsypal) Hajek & Gryganskyi, 2024

On adult Calliphoridae (Diptera): 'blue bottle flies' in Coah. (Mexico) (Sanchez-Peña 2000) and *Lucilia sericata* in NY (US) (B. Lovett unpubl. data).

Zoophthora

[66] Zoophthora aphrophorae (Rostr.) S. Keller, 2007

On the pine spittlebug, *Aphrophora parallela* (Hemiptera, Aphrophoridae), in PA (US) (Knull 1932).

[67] Zoophthora canadensis (MacLeod, Tyrrell & Soper) Remaud. & Hennebert, 1980

On Schizolachnus piniradiatae (Hemiptera, Aphididae) in red pine plantations in ON (Canada) (MacLeod et al. 1979).

[68] Zoophthora forficulae (Giard) A. Batko, 1964

On Forficula auricularia (Dermaptera, Forficulidae) in OR and WA (US) (Rockwood 1950; Hutchison 1963).

[69] Zoophthora geometralis (Thaxt.) A. Batko, 1964

On adults of *Eupithecia* sp., *Petrophora* sp., and *Thera* sp. (Lepidoptera, Geometridae) in ME (US) (Thaxter 1888).

[70] Zoophthora ichneumonis Bałazy, 1993

On an adult ichneumonid (Hymenoptera) in PA (US) (C. Tkaczuk, unpubl. data).

[71] Zoophthora independentia A.E. Hajek, Humber & Gryganskyi, 2016

Resting spore stages occurred within adult *Tipula submaculata* (Diptera, Tipulidae) in NY (US) (Hajek et al. 2016).

[72] Zoophthora occidentalis (Thaxter) A. Batko, 1964*

First reported on 'aphides on *Betula populifera*' in MA and ME (US) (Thaxter 1888). On aphids (Hemiptera, Aphididae), *Myzus persicae*, *Macrosiphum euphorbiae*, and *Aphis fabae* in ME (US); *Acyrthosiphon pisum* and *Aphis glycines* in NY (US); and *Sitobion avenae* in ID (US) (Feng et al. 1990; Nielsen and Hajek 2005; Barta and Cagáň 2006; ARSEF 2020).

[73] Zoophthora phalloides A. Batko, 1966

Aphid pathogens (Hemiptera, Aphididae) on *Macrosiphum euphorbiae*, *Nearctaphis bakeri*, *Uroleucon* sp., and *Acyrthosiphon pisum* in QC (Canada), ME and NH (US) (Remaudiére et al. 1978). On *A. pisum* in Oax. (Mexico) and *Therioaphis maculata* in Mexico (ARSEF 2020) and NY (US) (Milner and Soper 1981).

[74] Zoophthora phytonomi (Arthur) A. Batko, 1964*

Two genotypes infecting weevils in the genus *Hypera* (Coleoptera, Curculionidae) occur in North America (Hajek et al. 1995). The genotype principally infecting *Hypera postica* was first found in 1973 in ON (Canada) and subsequently in 21 eastern US states (Fig. 4). This genotype was also reported in *H. punctata* from NY (US). The second genotype infected *Hypera punctata* in ON (Canada) and NY and DE (US) (Hajek et al. 1995).



Figure 4. Distribution of recorded occurrences of *Zoophthora phytonomi* in the US and Canada (Hajek et al. 1995). Dark gray = states and provinces where this pathogen was reported from both *Hypera postica* and *Hypera phytonomi*; light gray = US states where this pathogen was only reported from *H. postica* (Hajek et al. 1995).

[75] Zoophthora porteri (R.S. Soper) A.E. Hajek, Humber & Gryganskyi, 2016

Resting spore stages occurred within adult *Tipula colei* (Diptera, Tipulidae) in TN (US) (Hajek et al. 2016).

[76] Zoophthora radicans (Bref.) A. Batko, 1964*

On hosts in diverse families across Hemiptera, Lepidoptera, Hymenoptera, and Diptera. Widespread distribution across the US, Canada, and Mexico (Table 11).

Table 11. Recorded arthropod hosts of Zoophthora radicans in the US, Canada, and Mexico.

Host Order	Host Family	Host Species	Country	States/ Provinces	References
Diptera	Drosophilidae	philidae -		FL	ARSEF 2020
	Nematocera	-	Mex	Dgo	Remaudière and Latgé 1985
	Tipulidae	-	US	ME	FPMI 1990
Hemiptera	Aphididae	Acyrthosiphon pisum	US	GA	Pickering et al. 1989
		Aphis nasturtii	US	ME	Shands et al. 1972
		Macrosiphum euphorbiae	US	ME	Shands et al. 1962
		Metopolophium dirhodum	US	ID, MT	Feng et al. 1990
		Myzus ornatus	Mex	-	Remaudière and Latgé 1985
		Sitobion avenae	US	ID	Feng et al. 1990
		Therioaphis maculata	US	NY	ARSEF 2020
		Therioaphis maculata	Mex	CDMX	FPMI 1990
		Therioaphis trifolii	Mex	CDMX	Remaudière and Latgé 1985
	Cicadellidae	Empoasca fabae	US	IL, MI, NY, WI	ARSEF 2020; McGuire et al. 1987
	Pentatomidae	Bagrada hilaris	Mex	Coah	Torres-Acosta et al. 2016
	Psyllidae	Trioza sp.	Can	QC	ARSEF 2020
		Psylla trimaculata	Can	QC	FPMI 1990
		Cacopsylla mali	Can	NS	Gilliatt 1925
	Triozidae	Bactericera cockerelli	Mex	Coah	Torres-Acosta et al. 2016

Host Order	Host Family	Host Species	Country	States/ Provinces	References
Hymenoptera	-	-	US	ME	ARSEF 2020
	Diprionidae	Neodiprion tsugae	US	AK	ARSEF 2020
Lepidoptera	Geometridae	Lambdina fiscellaria	Can	NF	Otvos et al. 1973
	Hesperiidae	Hesperiidae Thymelicus lineola		QC	FPMI 1990
	Noctuidae	Autographa precationis	US	IN	Yendol and Paschke 1987
		Rachiplusia ou	US	IN	Yendol and Paschke 1987
		Trichoplusia ni	US	IN	Yendol and Paschke 1987
		Trichoplusia ni	Mex	Coah	Sanchez-Peña 2000
	Plutellidae	Plutella xylostella	Mex	Gto	ARSEF 2020
	Tortricidae	Acleris variana	US	ME	ARSEF 2020
		Acleris variana	Can	NF	FPMI 1990
		Archips argyrospila	US	PA	Knull 1932
		Choristoneura biennis	Can	BC	FPMI 1990
		Choristoneura fumiferana	US	ME	Vandenberg and Soper 1975
		Choristoneura fumiferana	Can	BC, NS, ON	FPMI 1990
		Rhopobota naevana	US	MA	Sawyer 1933

[77] Zoophthora rhagonycharum (Bałazy) S. Keller, 2007

Resting spore stages in adult *Rhagonycha vilis* and *Rhagonycha fraxini* (Coleoptera, Cantharidae) in NY (US) (Hajek et al. 2024b).

Strongwellsea

[78] Strongwellsea castrans A. Batko & Weiser, 1965

On *Delia platura* (Diptera, Anthomyiidae) in WI (US) (Strong et al. 1960) and *Delia radicum* in ON (Canada) (Nair and McEwen 1973).

[79] Strongwellsea magna Humber, 1976

On Fannia canicularis (Diptera, Fanniidae) in CA (US) (Humber 1976).

FORM GENUS

Tarichium

[80] Tarichium megaspermum Cohn, 1875

On two species of Noctuidae (Lepidoptera): *Euxoa messoria* and *Euxoa ochrogaster* in BC and ON (Canada) (Bucher and MacLeod 1974; Steinkraus et al. 1993b).

Incomplete and questionable records

For some species we could not resolve the identification of the fungal species, especially older identifications based only on morphology or species for which confusion exists regarding the correct fungal species name to use. For example, the species *Entomophthora carpentieri*, named by Giard in 1888 from only resting spores collected in Europe, was identified by V.K. Charles from *Horistonus uhleri* (Coleoptera, Elateridae) collected in 1934 by J.N. Tenhet in SC (My-

CoPortal 2024). However, this fungal species is considered questionable by Keller (1991) and Bałazy (1993), and any potential synonymous species are not known in North America, and so it has not been included in this checklist.

One isolate of Entomophaga conglomerata is listed in the ARSEF culture collection (ARSEF 2020), but a recent publication demonstrated that this isolate instead belongs in the genus Batkoa (Gryganskyi et al. 2022b), and therefore this example was not included. Tipulids in NHand NC (US), collected by Thaxter, harbored a fungus named Entomophthora thaxteri (MacLeod and Müller-Kögler 1973), but this species was not adequately described. However, trying to find the correct genus and species for this species has been difficult. Over time, it has been suggested that this species could be E. conglomerata, Entomophaga tipulae, or Entomophthora tipulae (MacLeod and Müller-Kögler 1973; Bałazy 1993). In addition, because Thaxter found only resting spores in adults, perhaps this is Zoophthora independentia or Z. porteri. Therefore, this species (whatever it is) is not included in the checklist. In the case of Pandora blissi, this genus name is provided as nomen dubium; the native host of this species is no longer as abundant as in the past (Waldbauer 2005), and studies are currently underway to obtain specimens so the correct genus can be determined.

Sometimes, pathogen/host associations seem incorrect in initial reports. For example, in 1909, *Zoophthora radicans* was reported infecting the weevil *Hypera punctata* in IL (US) (Folsom 1909). However, now we know that *Zoophthora phytonomi* (not described until 1964) infects this weevil species in other regions (Fig. 4), and we have no examples of *Z. radicans* infecting Coleoptera (see Table 11). In this case, we have not included this location information under *Z. phytonomi* (Fig. 4) or under *Z. radicans* (Table 11).

Finally, as we do not include entries for which a species name has not been provided. Thus, we could not include an unidentified species infecting the economically important northern corn rootworm, *Diabrotica barberi* (Naranjo and Steinkraus 1988); in this case beetle cadavers only contained resting spores. We also could not include the only example from the Arctic. *Zoophthora* sp. was reported causing epizootics in outbreak populations of the noctuid *Eurois* occulta in West Greenland (Avery and Post 2013). The larval cadavers that had summited on the vegetation only contained resting spores, and the species could not be identified or described at that time.

Discussion

In 1963, a checklist of entomophthoralean fungi from the Western Hemisphere listed 39 species, all ascribed to the same genus: *Entomophthora* (Hutchison 1963). Today, with increased collection data and the incorporation of taxonomic changes within this group, our survey of arthropod pathogens in the Entomophthoromycotina found in North America includes 80 species in 14 genera, within 2 classes, plus one species in a form genus. A recent checklist of all fungi in North America (Bates and Miller 2018) lists only 38 arthropod-pathogenic species belonging to the Entomophthoromycotina. This checklist most likely relied on the Hutchison (1963) checklist, as it was the most recent available checklist for this group (Hutchison, 1963), underscoring the necessity for an updated checklist of Entomophthoromycotina in North America.

In their checklist for all North American fungi, Bates and Miller (2018) discuss the issue that there are many instances where European names were initially assigned to North American taxa based on morphological similarities. However, North American strains could represent cryptic taxa native to this continent that should be described as separate species, particularly if supported by molecular findings. We assume that this type of work will be undertaken in the future. However, at present many species in this group have not been isolated *in vitro* and/or there are no herbarium samples that can be used for DNA extraction. Therefore, to move forward along these molecular lines, in many cases, new specimens must be collected for analyses.

In fact, many species of arthropod pathogenic Entomophthoromycotina found worldwide have not been isolated in culture, and sequences are not available for molecular identification. In nature, viable cells of these fungi are quite ephemeral, and it is therefore difficult to collect them for isolation. The exception to this would be cadavers bearing resting spores (azygospores or zygospores). However, resting spores are often not found or, if found, are dormant and difficult to either germinate or use for DNA extraction (but see Bidochka et al. 1995; Eilenberg and Jensen 2018; Hajek et al. 2018). The ARSEF collection has North American cultures or samples from 29 of the species included in this checklist (approximately 36%). We hope that this annotated checklist will make it more possible in the future for the culture and sequencing of additional species in North America.

Taxonomic changes in this group have been relatively frequent since the first publication on species of Entomophthoromycotina in the United States by Thaxter in 1888, referring to this group as the Entomophthoreae. These taxonomic changes pose challenges for understanding whether names for host/fungus associations in the older literature are accurate today. For example, E. muscae is now known to be a species complex (Elya and De Fine Licht 2021), with one species named E. muscae s.s delimited within the complex. Therefore, for older records when E. muscae is mentioned, it is unclear which of the species in the complex is being discussed and how to apply historical findings to the modern circumscription of the species E. muscae itself. Therefore, since this checklist treats the three species of this species complex known from North America separately, the older reports of E. muscae have usually not been included in order not to introduce errors. The Entomophaga grylli species complex raised similar problems. Today, two members of this complex occur in North America, and older literature did not differentiate between them, with the result that older reports for collection locations could not be included.

Likewise, confusion has occurred with *Pandora neoaphidis*, for which the correct nomenclature was only resolved in 1980 (Barta and Cagáň 2006). From 1888 (Thaxter) until 1980, in North America, *P. neoaphidis* was incorrectly known as *Empusa aphidis* and later *Entomophthora aphidis*. However, in 1980 *Entomophthora aphidis* was synonymized with *Zoophthora aphidis*, a species known only from relatively few host aphids in western and central Europe. We assume that records of *Empusa* or *Entomophthora aphidis* in North America before 1980 probably refer to *P. neoaphidis*, especially for collections from Maine, due to the common occurrence of *E. aphidis* and the presence of cultures of *P. neoaphidis* from Maine collected in 1972 and 1977 in the ARSEF collection (ARSEF 2020).

Our records of the distribution of fungal species are predominantly based on reports in the literature. The time of year, or even year of collection, is not always reported. Additionally, entomophthoralean fungi have been collected by only a handful of experts and remain vastly understudied across many locations in North America. Therefore, if a state or province is not listed, this is not definitive proof that a species is not present there, but rather this suggests that further surveys are necessary.

This annotated checklist provides data on these arthropod pathogens by connecting arthropod host species and fungal species at different locations within North America. Therefore, for each record, three specific pieces of information were needed: 1) host species, 2) fungal species, and 3) collection location. Unfortunately, some publications (although relatively few) did not provide separate data for these three metadata types and thus could not be included. Such problems arose with Remaudière et al. (1978), where all fungal pathogens and their aphid hosts were merged for one trip covering NH (US), and ON and QC (Canada). Similarly, we could not include data from Feng et al. (1990), in which data from collections of three species of aphid-pathogenic *Conidiobolus* species were merged so that locations and hosts of individual species were not listed (one of these species is now a *Batkoa*), or from Wraight et al. (1993), in which data for fungal infections of several cereal aphid species were merged.

Conclusion

In conclusion, we provide an updated checklist of arthropod pathogenic fungi in the Entomophthoromycotina detected in North America, using the latest taxonomy and largely based on published literature. While this checklist includes many more species than the last checklist (Hutchison 1963), there are still many arthropod-pathogenic species known from this subphylum (see Sacco and Hajek 2023) that have not been found in North America. Additional sampling is needed to determine if these are truly absent from the continent or await discovery as well as whether new discoveries await. Additionally, given the paucity of molecular data (De Fine Licht et al. 2016), sequencing of additional species from verified specimens, together with improved taxonomies, is an area of future research that will enhance DNA-based identification of these fungi. This updated checklist provides a framework for future efforts sampling and documenting the biodiversity of this important, yet understudied, group of fungi.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: AEH. Data curation: AEH, KLS, CT, SSP. Formal analysis: AEH. Funding acquisition: KEB. Investigation: AEH, SSP, CT. Methodology: AEH. Project administration: AEH. Software: BL, KLS. Supervision: KEB, AEH. Validation: AEH. Visualization: KLS, BL. Writing - original draft: AEH. Writing - review and editing: CT, SSP, KLS, AEH, BL, KEB.

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Data availability

All of the data that support the findings of this study are available in the main text.

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